

A NEW DICYNODONT REPTILE FROM THE *TAPINOCEPHALUS* ZONE (KAROO SYSTEM, BEAUFORT SERIES) OF SOUTH AFRICA, WITH EVIDENCE OF THE JAW ADDUCTOR MUSCULATURE

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(With 7 figures)

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ABSTRACT

A new dicynodont, *Chelydontops altidentalis*, from the farm Die Cypher, Beaufort West, South Africa, is described from an incomplete skull and jaw in the South African Museum. Important characteristics of the new form are the wide intertemporal region, the vaulted anterior part of the secondary palate, the well-developed rows of teeth on the palate and dentary, and a low but distinct coronoid process of the lower jaw. Upper and lower tooth rows are bounded laterally by bony platforms, whose function is discussed in terms of jaw musculature and mastication. The coronoid process on the lower jaw indicates that the medial external adductor muscle of the lower jaw inserted on the rear of the dentary, as in the advanced pelycosaur *Dimetrodon*. It is postulated that the dorsal surface of the dentary, lateral to the tooth row, and the platform on the maxilla, lateral to the palatal tooth row, indicate the presence in life of a reptilian cheek, such as recently proposed for certain ornithischian dinosaurs. Similar but relatively larger palatal and dentary platforms are found in the chronologically younger *Endothiodon* (including *Esoterodon*, *Emydochamps* and *Endogomphodon* as junior synonyms) and *Pachytegos*, and it is proposed that the subfamily Endothiodontinae be enlarged to include *Chelydontops* and *Prodicynodon*. In terms of jaw function, these genera appear to be distinct from other dicynodont groups.

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INTRODUCTION

In his treatment of the South African *Tapinocephalus* zone Dicynodontia, Boonstra (1948) briefly mentioned an unprepared skull (SAM-11558) which he considered might eventually prove to be a new endothiodont. The specimen, from the farm Die Cypher, Beaufort West, has recently been fully prepared and clearly represents a new type of dicynodont, with *Endothiodon* and possibly *Prodicynodon* its closest allies. A second specimen, a skull and jaw (SAM-12259) from Beukesplaas, Fraserburg, is generally similar to the Die Cypher

skull, but differs in some respects; lateral crushing of this specimen has made a close comparison with SAM-11558 difficult, and it has been used chiefly to provide supplementary information in areas lacking in the type.

The dicynodonts of the *Tapinocephalus* zone were last reviewed by Boonstra (1948) and Toerien (1953), but in the light of new classificatory criteria (Hotton & Cluver, in preparation), the group is once more under investigation by the present author. The specimens described and discussed below are, however, systematically sufficiently far removed from their contemporaries to warrant a separate, independent account.

SYSTEMATICS

As yet no satisfactory dicynodont classification exists. However, the following scheme, modified from Houghton & Brink (1954) and Romer (1966), may serve to indicate the systematic position of the form under consideration.

Class	: Reptilia
Order	: Therapsida
Suborder	: Anomodontia
Infraorder	: Dicynodontia
Family	: Endothiodontidae
Subfamily	: Endothiodontinae

Chelydontops gen. nov.

Diagnosis

Skull with wide intertemporal region and broadly exposed parietals. Pineal opening large and situated on high boss. Maxilla rising high in snout, septomaxilla entirely within nostril. Caniniform process rudimentary, vestigial caniniform tooth may be present. No anterior palatal ridges, anterior premaxillary part of palate deeply vaulted. Palatine large, meeting premaxilla. Posterior, palatal portion of maxilla raised to form prominent ledge, with medial crest bearing nine robust teeth. Choanal vault wide and deeply recessed, vomers forming narrow anterior septum. Long interpterygoidal vacuity. Medial edge of dentary bearing row of ten teeth. Dentary extended posterodorsally as a clear coronoid process.

Chelydontops altidentalis gen. et sp. nov.

Diagnosis: As for genus.

Type: Snout, occiput, partial lower jaw and cervical vertebrae in South African Museum, Cape Town (Cat. No. 11558).

Locality: Die Cypher, Beaufort West, Cape Province.

Horizon: *Tapinocephalus* zone, Beaufort Series.

Collector: L. D. Boonstra.

DESCRIPTION OF THE MATERIAL

Type specimen (SAM-11558)

Skull

The skull is represented by the major portion of the snout and the occipital segment up to the anterior border of the pineal foramen (Figs 1, 2, 3A). In the skull roof the frontals, postorbital bars and zygomatic arches are lacking, while in the ventral midline there is a gap in the pterygoid-basisphenoid central stem at the level of the internal carotid artery foramina. There is thus no contact between the front and rear halves of the skull, but as both portions agree completely in size, in colour and in texture of bone and matrix, and were (apparently) in close association when collected, there seems no reason to doubt that they represent parts of a single individual.

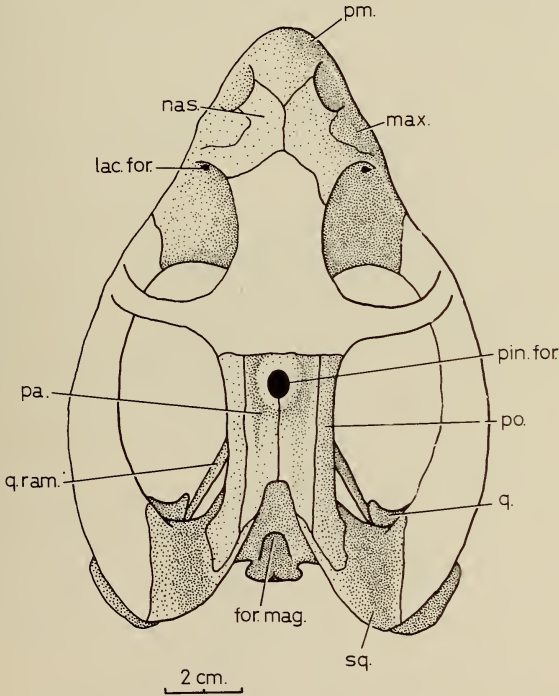


Fig. 1. *Chelydontops altidentalis* gen. et sp. nov. Skull reconstructed in dorsal view, missing areas shown in outline. One-half natural size.

In the snout the premaxilla is smoothly curved and slopes far back between the nasals. Behind the nostril the maxilla extends up to meet the nasal, and the septomaxilla is confined to within the nostril. The nasals form low bosses above the nostrils. Although neither side of the palatal rim is completely

preserved, it is evident that no distinct caniniform process was present. On both sides the base of a small marginal tooth is visible.

The lacrimal is a large bone in the antero-ventral corner of the orbit; a short anterior process extends forwards on to the side of the snout to meet the nasal in front and the maxilla below (Fig. 3A). The snout is not preserved above this level, and the relationships of the frontals and pre-frontals could not be determined. However, the base of the zygomatic arch can be seen clearly in section on both sides. A large maxillary antrum is enclosed between the jugal and lacrimal, and these two bones are in turn supported anteriorly and ventrally by the maxilla and ectopterygoid. As in most dicynodonts, a large opening between the inner edges of the lacrimals, jugals and palatines leads forward from the orbital region into the bony nasal chamber.

The palate is marked by several distinctive features (Figs 2, 4). The palatal rim is low and carries a weakly developed tooth in its rear, maxillary part. There are no anterior palatal ridges on the premaxilla, but medially this bone carries a prominent posterior ridge which meets the forked anterior edge of the vomer. The anterior part of the palate and palatal rim is incomplete, but it can nevertheless be seen that the premaxilla is deeply recessed in the anterior midline so that, when complete, the secondary palate would have featured a

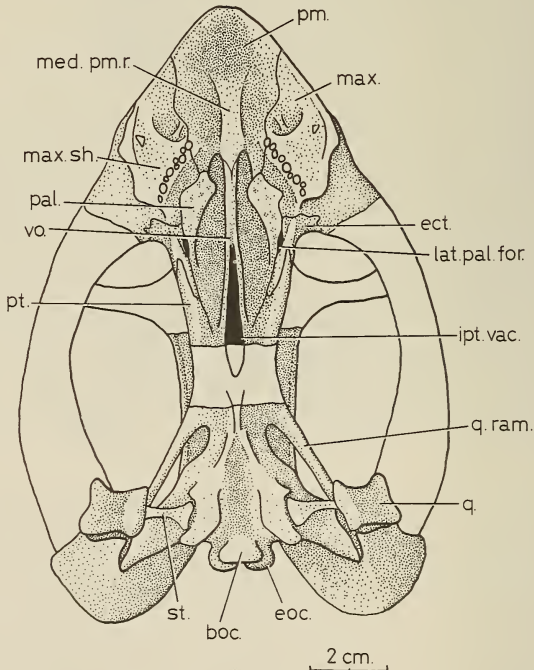


Fig. 2. *Chelydontops altidentalis* gen. et sp. nov. Skull reconstructed in ventral view, missing areas shown in outline. One-half natural size.

high and narrow anterior vault. Much of the secondary palate is made up by the premaxilla which, extending back to meet the anterior tip of the palatine, excludes the maxilla from the choana. In palatal view, both premaxilla and palatine are raised above the level of the adjoining maxilla, while laterally there is a raised platform-like area on the maxilla medial to the posterior part of the palatal rim (Fig. 2, max. sh.). This maxillary shelf, together with the palatal rim, extends backwards to terminate posteriorly as a sharply defined crest below the base of the zygomatic arch. The medial edge of the raised area bears an irregular row of nine teeth, of which a few are newly erupted. The fully developed teeth are relatively powerful, and the row extends back 17 mm from the premaxilla-maxilla suture (where the base of the leading tooth is at least partly surrounded by premaxilla) to the posterior limit of the maxillary shelf.

The palatal portion of the palatine is large and raised above the surface of the surrounding premaxilla and maxilla. Posteriorly it lies high in the side wall of the choana, medial to the ectopterygoid. This latter bone is strongly

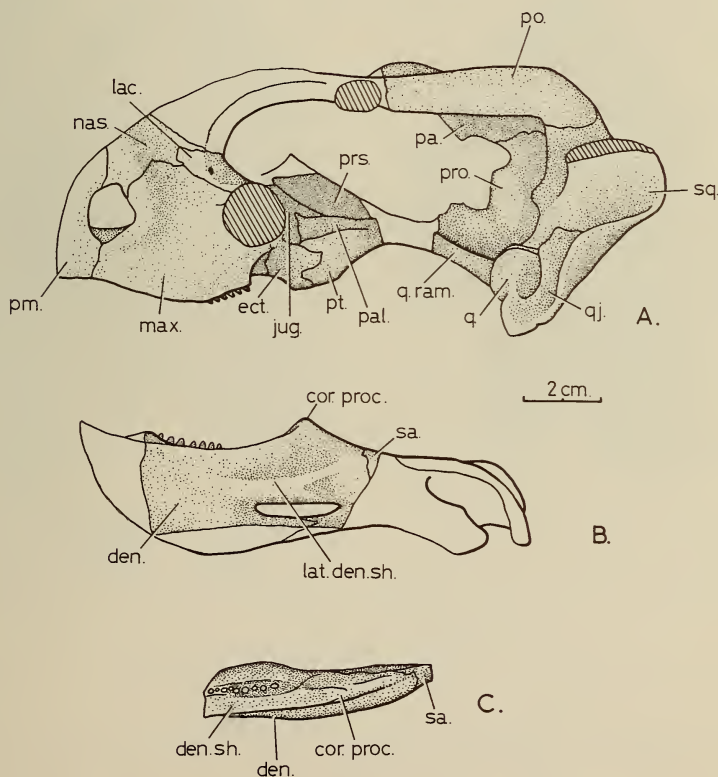


Fig. 3. *Chelydontops altidentalis* gen. et. sp. nov. A. Skull reconstructed in lateral view, missing areas shown in outline. B. Lower jaw fragment in lateral view and (C) in dorsal view. All one-half natural size.

developed, and consists of a lateral sheet, which lies beneath the base of the zygomatic arch, and a posterior portion, which helps form part of the lateral wall of the choana and appears to clasp the anterior edge of the pterygoid. This section of the choanal side wall, composed of palatine, ectopterygoid and pterygoid, is deep and the choana, seen as a whole, is a very wide and deeply vaulted structure.

Behind its junction with the premaxilla, the vomer divides the internal nares as a high, median septum, but postero-dorsally it bifurcates to enclose the anterior part of the large (but incompletely preserved) interpterygoidal vacuity.

In the occipital section the intertemporal part of the skull roof is preserved up to the anterior margin of the pineal foramen. The postorbitals are well separated by the parietals (Fig. 1) and lie mainly along the lateral margins of the temporal roof. The broadly exposed parietals form a prominent boss



Fig. 4. Stereophotograph of palate of *Chelydontops altidentalis* gen. et sp. nov.

around the pineal foramen. The occiput is high, with the tripartite condyle set at a relatively low level. A pair of deep basioccipital tubera, separated by a median cleft, is present, and on the left side a slender stapes is partially preserved. The squamosal, supporting the quadratojugal and quadrate ventrally, is of the usual triradiate, dicynodont type.

Lower jaw

The middle portion (Fig. 3B, C) of each dentary is preserved and on the left side the articular is in natural articulation with the quadrate. In each jaw ten well-developed teeth are present, lying in an irregular row on the inside of the dorsal edge of the dentary. A row of posterior serrations can be seen in several of these teeth. Lateral to the tooth row the dorsal dentary surface is a flat shelf (Fig. 3C, den. sh.), gently concave in lateral view. At the level of the anterior dentary teeth, the inside edge of the dorsal dentary shelf is raised to form the beginning of a high crest, which would have continued on to the missing symphyseal region. Posteriorly the shelf extends past the end of the tooth row and terminates on the anterior face of a small coronoid process, unique in dicynodonts. From the tip of this coronoid process the dentary slopes back and down to meet the surangular.

A fairly distinct lateral dentary shelf (Fig. 3B, lat. den. sh.), for insertion of the lateral portion of the external adductor muscle, is present and overlies a long and narrow mandibular fenestra. The articular of the left side, in contact with the quadrate, appears to be of the normal dicynodont pattern.

SAM-12259

Lateral compression in this specimen has obscured some details of the intertemporal region and palate, but there are strong resemblances with the type specimen in the nature of the palatal rim, the maxillary part of the secondary palate and the dentary.

The palatal rim is complete, and only a very modest caniniform process is present. Somewhat behind the process is a marginal tooth, at the level of the anterior choanal embayments. Medial to this the maxillary is thickened to form a distinct platform, similar to that of the type specimen, and carries a number of robust teeth along its inner border. Two large teeth and one smaller one are present on the right-hand side, while on the left side there are three or possibly four teeth; crushing and dislodging of the teeth of both upper and lower jaws on this side has made an exact assessment of the tooth number difficult.

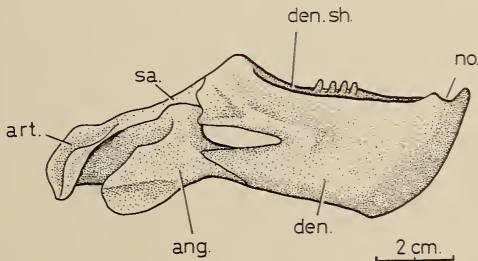


Fig. 5. *Chelydontops*?sp. SAM-12259. Mandible in lateral view. One-half natural size.

As in the type, the palatal rim and maxillary platform lateral to the teeth are extended back to a clearly marked termination below the base of the zygomatic arch.

As far as can be seen, the anterior part of the palate slopes up fairly steeply in front of the median premaxillary ridge, but lateral compression has made the extent of this vaulting uncertain. More posteriorly, the pterygoids and ectopterygoids of each side form a deep side wall to the choana, but the shape of the vomer and the exact forward extent of the palatine is not clear.

The lower jaw (Fig. 5) is well preserved, and closely resembles what remains of the type jaw. On the dorsal surface of the dentary there is a long, wide and shallow trough, bounded by a distinct coronoid process posteriorly and by sharp edges medially and laterally. The medial edge carries a row of four teeth, which show a series of fine posterior serrations. In front of these teeth the medial edge of the dentary is continued forwards for a short way as a sharp crest, which merges anteriorly with the dorsal surface of symphysis.

At the symphysis the dorsal surfaces of the two jaw rami are separated by a median cleft, but the front of the jaw is a fairly high and sharp blade, notched on each side (Fig. 5, no.).

JAW MUSCULATURE AND FUNCTION IN *CHELYDONTOPS*

JAW MUSCULATURE

Crompton & Hotton (1967) have reconstructed the jaw musculature of the dicynodonts *Emydops* and *Lystrosaurus*, and have analysed the probable range of jaw movements during mastication. A few modifications of their interpretations have been suggested by Cluver (1971, 1974), these pertaining chiefly to the crushing role played by the dentary during the final stages of the mastication cycle, and to the insertion areas on the lower jaw of the jaw adductor muscle fibres. Recently Barghusen (1968, 1972, 1973) has published a series of important papers dealing with the adductor musculature and jaw mechanics in both primitive and advanced synapsids, and many of his findings are relevant to considerations of dicynodont jaw musculature.

Areas of origin of jaw adductor muscles

In dicynodonts the highly modified temporal region provides two large areas of origin for the external adductor musculature. An inner division, the medial external adductor muscle, arose from the lateral, posterior and medial borders of the temporal fossa, these areas being formed by the squamosal and postorbital (Fig. 6B). The outer surface of the postorbital, forming the dorsal, inner border of the temporal fenestra, merges smoothly with the upper surface of the squamosal, where this bone forms the posterior border of the fenestra. This surface is continued laterally and forward on to the inside of the zygomatic arch, and in this way an extensive area of origin is formed.

Laterally to the temporal fossa the squamosal extends back and outwards as a characteristic external plate below the rear of the zygomatic arch. The anterior surface of this smoothly moulded sheet is continued dorsally on to the lateral face of the zygomatic arch, and includes the anterior face of the quadratojugal ventrally. This substantial area served for the origin of the lateral external adductor muscle (Fig. 6C), and among therapsids is found only in dicynodonts.

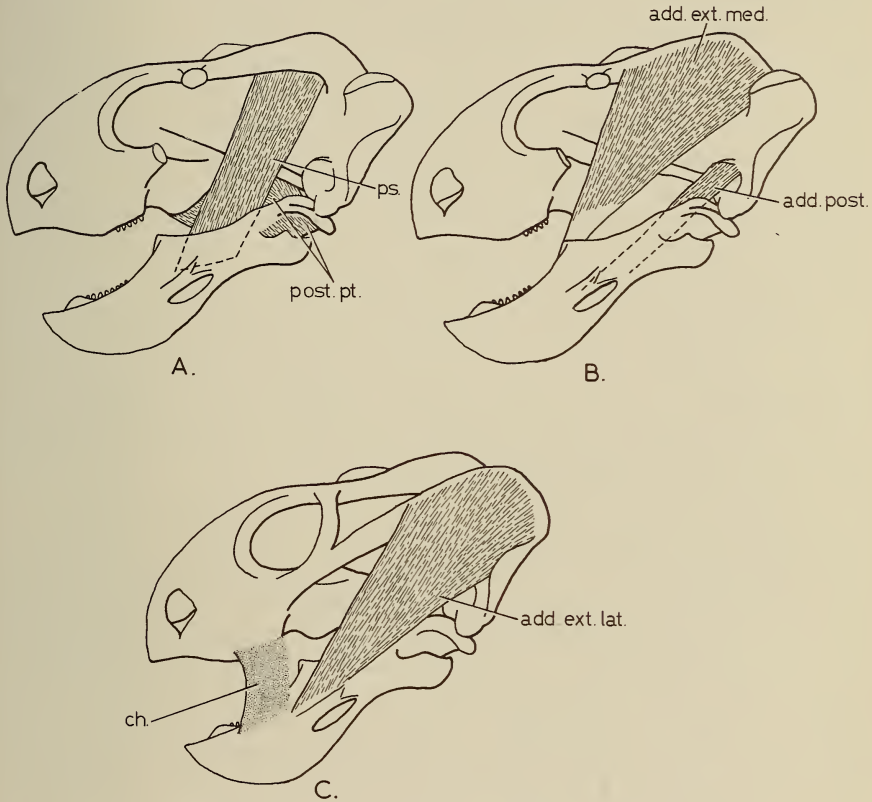


Fig. 6. *Chelydontops altidentalis*. Skull reconstructed in lateral view to show (A) pseudotemporalis and posterior pterygoideus muscles, (B) medial external adductor and posterior adductor muscles and (C) lateral external adductor muscle and cheek.

The degree of development of the intertemporal part of the skull roof varies considerably in dicynodonts. In a genus such as *Daptocephalus* the parietals are greatly reduced on the skull roof and the postorbitals approach each other closely (Ewer 1961), while in cistecephalids (Keyser 1973; Cluver 1974) the parietals are broad elements and the postorbitals and temporal fenestrae are widely separated. However, a constant feature in all dicynodonts is a clearly demarcated recess beneath the lateral edge of the inter-temporal

skull roof, bounded medially by a ventral flange of the parietal and, more anteriorly, by the expanded dorsal part of the epipterygoid. This recess is similar in position to the 'medial depression' described by Barghusen (1973: 829) in the undersurface of the skull roof of the advanced pelycosaur *Dimetrodon*. Barghusen considered the depression to be the site of origin of the pseudotemporalis muscle of the internal jaw adductor group (Fig. 6A, ps.), which presumably also attached to the epipterygoid and parietal.

In addition, the area of origin of a posterior adductor muscle, also part of the internal jaw adductor musculature, can be inferred. In recent reptiles this muscle arises from the medial part of the quadrate bone, and Barghusen (1973: 831) reconstructs it in *Dimetrodon* as arising from 'the lateral face of the well-developed anterior process of the quadrate which contacts the pterygoid bone'. In a dicynodont such as *Chelydontops* the portion of the quadrate above the condyle is a high and broad sheet lying up against the squamosal and the posterior end of the quadrate ramus of the pterygoid, and is well situated to serve as a site of origin of a muscle, such as the posterior adductor, running to the inside of the lower jaw (Fig. 6B, add. post.).

In dicynodonts, the posterior pterygoideus muscle (*sensu* Barghusen 1973) of the internal adductor group very likely arose from the ventro-lateral edge of the pterygoid, where this forms the lateral boundary of the choana, and from the pterygoid's quadrate ramus (Fig. 6A, post. pt.). Such a posterior pterygoideus muscle would include both the anterior and posterior pterygoideus muscles of Crompton & Hotton (1967) and Cluver (1971).

Areas of insertion of jaw adductor muscles

The adductor musculature's attachment areas on the lower jaw are more clearly indicated in *Chelydontops* than in other dicynodonts. It seems most likely that the lateral dentary shelf, present in varying degrees of prominence above the mandibular fenestra in all dicynodonts (Crompton & Hotton 1967; Cluver 1970, 1971, 1974) marks the site of insertion of the lateral external adductor muscle (Fig. 6C). Such a purely lateral insertion area corresponds well with the lateral position of the area of origin of this muscle in dicynodonts. The insertion area of the medial external adductor muscle in *Chelydontops* is of special significance. The low but distinct coronoid process on the rear end of the dentary is strong evidence of a tendinous attachment, and it seems very likely that the large medial division of the external adductor muscle (Fig. 6B) inserted on to the lower jaw via a 'bodenaponeurosis', such as reconstructed by Barghusen (1973) in *Dimetrodon*, on the basis of comparisons with recent reptiles. This is in contrast with Crompton & Hotton's (1967) restoration, according to which the medial external adductor muscle inserts into a deep groove in the dorsal edge of the dentary behind the symphyseal region.

The pseudotemporalis muscle appears to have had a fleshy attachment on the inside of the lower jaw above the adductor (Meckelian) fossa. In *Chelydontops* the surangular and rear part of the dentary are smoothly excavated

above this fossa and, in fact, it is likely that it was to accommodate a changed orientation of the pseudotemporalis muscle that the dorsal part of the lower jaw is bowed laterally in cistecephalids (Cluver 1974).

The adductor posterior muscle, arising from the anteromedial face of the quadrate, has a clear insertion site in and around the adductor fossa, while the pterygoideus posterior muscle (Fig. 6A) extended to the lower edge of the jaw and inserted on the lateral face of the angular, at least partly beneath the reflected lamina (Crompton & Hotton 1967; Cluver 1971; Barghusen 1973). A posterior slip of this muscle probably inserted on the inner surface of the retroarticular process.

With one exception, the jaw adductor musculature thus reconstructed in *Chelydontops* is essentially comparable with that restored in *Dimetrodon* by Barghusen (1968, 1973) and is readily derivable from a reptilian model. The exception is the lateral division of the external adductor muscle, this representing a basic dicynodont innovation. Moreover, it seems probable that the insertion of the medial external adductor in *Chelydontops* is typical in its position (although exaggerated in form) since the rear end of the dentary was the most anterior area of insertion of the external adductor muscle in primitive synapsids (Barghusen 1973).

In *Chelydontops* the slightly excavated dorsal surface of the dentary behind the symphysis may be compared with the deep dorsal dentary groove seen in some other dicynodonts (Crompton & Hotton 1967; Cluver 1970, 1971) but, lying as it does in front of the coronoid process and directly lateral to the tooth row, it seems unlikely that it served as an area of muscle attachment. In *Chelydontops* this part of the dentary should more properly be considered in conjunction with the raised area of maxilla lateral to the row of palatal teeth. As shown below, it is unlikely that more than the most medial part of this platform was directly involved in any chewing activity and, in effect, there is a space between the upper and lower tooth rows and the side of the snout. This structural arrangement is perhaps best explained in terms of the development of a reptilian cheek, such as reconstructed by Galton (1973) in certain ornithischian dinosaurs which show evidence of similar platforms lateral to the tooth row. In *Chelydontops*, evidence suggesting the presence of a cheek consists of the crest running back from the weak caniniform process to the rear of the maxillary platform. This crest can be interpreted as marking the dorsal line of attachment of the cheek, while its ventral attachment was most likely along the sharp lateral edge of the dorsal dentary platform. A cheek of this sort would have occupied more or less the same position as the 'Mundplatt' reconstructed by Crompton & Hotton (1967) in *Emydops*. In fact, modification of the reptilian 'Mundplatt' offers a simple derivation for the cheek reconstructed in *Chelydontops* (Fig. 6C).

The actual structure of the cheek reconstructed for *Chelydontops* is uncertain, but the possibility that it was muscular does exist. Galton (1973) suggests that musculature in his reconstructed ornithischian cheek might easily

have been derived from either the reptilian levator angularis oris muscle, or the pars superficialis of the reptilian external adductor jaw musculature—a similar derivation is possible in *Chelydontops*. Crompton & Hotton (1967) reconstructed a levator oris muscle arising from the infraorbital bar in *Emydops* and inserting on the 'Mundplatt'. As shown by Galton (1973) it is not necessary to draw an analogy with mammals to postulate the presence of a muscular cheek in reptiles. When a mammalian type muscular cheek, innervated by the facial nerve, arose is uncertain; if such an event occurred in therapsids, it may have been a late development in the most progressive of therapsid lines, i.e. the cynodonts.

JAW FUNCTION

Cheek function in a reptile such as *Chelydontops* should be considered in conjunction with the probable range of jaw movements during the masticatory cycle. As shown by Crompton & Hotton (1967), the power stroke during dicynodont mastication occurred during retraction of the lower jaw, and this would certainly have been true in *Chelydontops*. While some slicing would very likely have occurred between the lateral sides of the lower jaw beak and the palatal rim, the batteries of powerful mandibular and palatal teeth suggest that considerable slicing and cutting between these teeth took place towards the end of the stroke. Both upper and lower tooth rows (best preserved in the type specimen) are obliquely orientated, with the anterior teeth of each row lying medial to the posterior teeth. Upper and lower tooth rows are practically the same distance apart, and it is apparent that strictly orthal retraction would cease when the mandibular tooth rows meet the palatal tooth rows in face-to-face contact. This arrangement would prevent the mandibular teeth from immediately reaching the inflated palatal portions of the palatines, so obviously involved in the mastication process in other dicynodonts (Crompton & Hotton 1967; Cluver 1971).

A sideways displacement of the mandible on the quadrates, to permit the upper and lower tooth rows to slide past each other, would result in a complex series of tooth-to-tooth and tooth-to-beak contacts coming into play, during which only one palatine at a time would be involved. However, movement of this type would be possible only if the articulation between the quadrate and lower jaw lacked the tightly interlocking articular facets seen in most dicynodonts (Cluver 1974). Since, as far as can be seen, this is not the case in *Chelydontops*, an alternative possibility involving two separate phases of masticatory activity may be considered. Thus, apart from a shearing phase during which the lower jaw is drawn back from a protracted position until the mandibular teeth meet the palatal tooth rows, a purely up-and-down biting action, involving both tooth rows and the palatines, could have taken place with the lower jaw in an almost fully retracted position.

With only incomplete material available, the range of lower jaw movements during mastication must remain uncertain, but it seems clear that the upper and

lower tooth rows played an important part in the process. Retention of, and control over, partly chewed plant matter, which would tend to move to the side of the mouth, could become a critical factor, and the need for a cutaneous or muscular sheet in the corner of the mouth might very likely arise. A non-contractile cheek would serve merely to retain masticated food until this could be drawn back into the oral cavity by the tongue. A muscular cheek would be capable of actively assisting in mastication by returning partly-chewed material to the teeth. It is noteworthy that only in forms where the palatal and mandibular teeth are strongly developed, such as *Chelydontops* and *Endothiodon*, is a lateral maxillary shelf formed; to this extent, jaw function sets these genera apart from other dicynodonts.

AFFINITIES OF *CHELYDONTOPS*

In several of its characters *Chelydontops* closely resembles members of the sub-family Endothiodontinae, which, according to Cox (1964), includes the genera *Endothiodon* (with *Esoterodon*, *Emydochampsia* and *Endogomphodon* as junior synonyms) and *Pachytegos*, the latter from the Ruhuhu Valley of Tanzania. Resemblances between *Chelydontops* and *Endothiodon* involve features of the palate and mandible. Thus, the anterior part of the secondary palate in *Endothiodon* is deeply vaulted as in *Chelydontops*, and there is no true caniniform process. A ventral process of the anterior, premaxillary part of the palatal rim, characteristic of *Endothiodon*, is seen also in SAM-12259—this portion of the palatal rim is incomplete in the *Chelydontops* type specimen. Prominent features in both the palate and mandible of *Endothiodon* are the wide and shallow troughs lying lateral to the upper and lower tooth rows. In the palate (Fig. 7A) this is especially marked, and the shelf of each side is bounded by a distinct crest which is extended back and outwards below the zygomatic arch as in *Chelydontops*. Cox (1964) mentions this feature, which may be regarded as an expanded equivalent of the maxillary platform of *Chelydontops* and indication of a fairly extensive cheek. The palatal part of the premaxilla in *Endothiodon* also extends far back, but does not meet the palatine as it does in *Chelydontops*. A point of importance is the rooting in *Endothiodon* of the first two palatal teeth in the rear of the premaxilla. Unfortunately it was not possible to determine with certainty whether the first tooth in *Chelydontops* is placed in the premaxilla in the same way, but it is clear that at least part of the base of this tooth is surrounded by the premaxilla.

Although these are for the most part important resemblances, *Chelydontops* differs sharply from *Endothiodon* in the retention of a broad intertemporal region, with widely exposed parietals, and also in the apparently smoothly rounded snout, without the longitudinal ridges so characteristic of the dorsal surface of the *Endothiodon* snout.

Besides *Endothiodon*, *Chelydontops* shares several features with the poorly-known genus *Prodicynodon* (Broom 1912). The type specimen of *Prodicynodon*

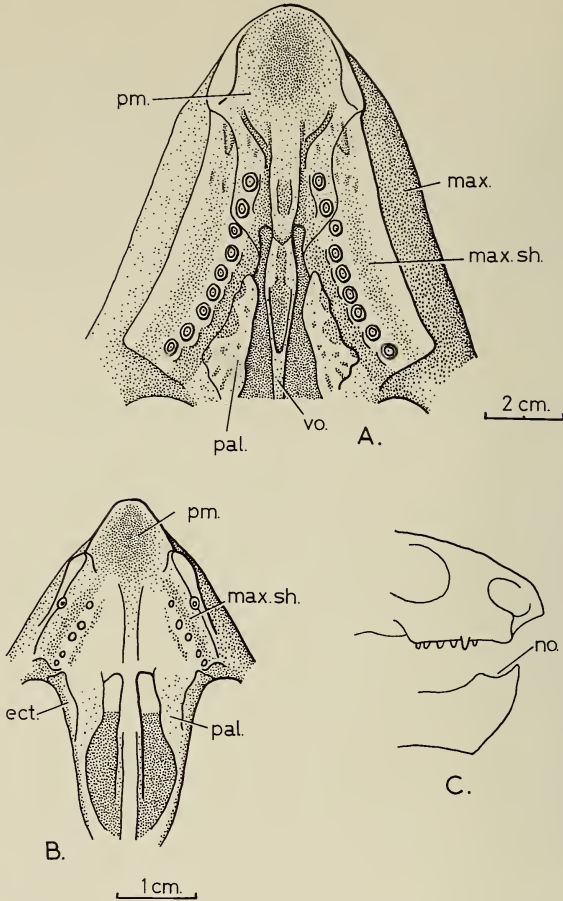


Fig. 7. *Endothiodon uniseriis* BMNH-49414. Palatal reconstruction of type specimen. B. *Prodicynodon beaufortensis* AMNH-5509. Palatal reconstruction of type specimen. Both one-half natural size.

pearstonensis (AM-2551) is too crushed and incomplete to allow adequate comparisons to be made, but recent preparation of the type specimen of *P. beaufortensis* (AMNH-5509) shows that in addition to the pointed anterior beak of the lower jaw, typical of *Endothiodon* (Cox 1964), this form has a row of *Endothiodon*-like teeth bounded laterally by a wide, shallow trough (Fig. 7B). A small marginal tooth lies on the palatal rim, in the same position as in *Chelydontops*, and a caniniform process is absent. However, a weak ventral process at the maxilla-premaxilla meeting on the palatal rim resembles that of *Endothiodon* and *Chelydontops*. In the palate the premaxilla is vaulted in the endothiodontinid manner to receive the anterior tip of the lower beak, while a notch behind this anterior tip is reminiscent of the condition in SAM-12259.

Cox (1964) recognizes two genera in the subfamily Endothiodontinae, these being *Endothiodon* itself, from the Endothiodon zone (*Cistecephalus* zone of Kitching 1970) and *Pachytegos* from the Ruhuhu Beds of Tanzania. It now seems necessary to include *Chelydontops* and *Prodicynodon* in this subfamily. *Prodicynodon pearstonensis* is from Pearston, and *Prodicynodon beaufortensis* is from Kuilspoort, Beaufort West; both are probably from *Endothiodon* zone (Kitching's *Cistecephalus* zone) strata. *Chelydontops*, from the *Tapinocephalus* zone of Beaufort West, represents the earliest known member of this distinctive group of dicynodonts.

SUMMARY

The skull and mandible of *Chelydontops altidentalis* from the *Tapinocephalus* zone of the Beaufort Series show strong affinities with *Endothiodon* and *Prodicynodon*, and, together with *Pachytegos* of Tanzania, these three genera should be included in the subfamily Endothiodontinae. While several conservative characters and its low stratigraphic occurrence make *Chelydontops* a primitive (but not necessarily ancestral) member of the subfamily, a functional reconstruction of the skull helps interpret the characteristic skull structure of the group as a whole. A clear coronoid process on the dentary allows a reconstruction of the external jaw adductor muscles to be made with fair confidence, while a shelf lateral to each upper tooth row is taken as indication of the former presence of a reptilian cheek, such as has been recently proposed for ornithischian dinosaurs. There is a possibility that fibres from either the levator angularis oris or adductor externus lateralis muscles had invaded the primarily non-contractile cheek, which was very likely derived from a reptilian 'Mundplatt'.

With the identification of *Chelydontops altidentalis*, the *Endothiodon* grade of dicynodont development can be traced farther back into the Permian than before, and since the functional innovations seen in *Chelydontops* are continued and improved upon in the later genera, this grade can now be more closely defined and better understood.

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REFERENCES

- BARGHUSEN, H. R. 1968. The lower jaw of cynodonts (Reptilia, Therapsida) and the evolutionary origin of mammal-like adductor jaw musculature.—*Postilla* 116: 1–49.
- BARGHUSEN, H. R. 1972. The origin of the mammalian jaw apparatus. In: G. H. SCHUMACHER. *Morphology of the maxillo-mandibular apparatus*: 26–32. Leipzig: VEB Georg Thieme.
- BARGHUSEN, H. R. 1973. The adductor jaw musculature of *Dimetrodon* (Reptilia, Pelycosauria).—*J. Paleont.* 47: 823–834.
- BOONSTRA, L. D. 1948. On the anomodont reptiles from the *Tapinocephalus* zone of the Karroo System. In: ROYAL SOCIETY OF SOUTH AFRICA. *Robert Broom commemorative volume*: 57–64. Cape Town: Royal Society of South Africa. (Special publication.)
- BROOM, R. 1912. On some fossil reptiles from the Permian and Triassic beds of South Africa.—*Proc. zool. Soc. Lond.* 1912: 859–876.
- CLUVER, M. A. 1970. The palate and mandible in some specimens of *Dicynodon testudirostris* Broom & Haughton (Reptilia, Therapsida).—*Ann. S. Afr. Mus.* 56: 155–274.
- CLUVER, M. A. 1971. The cranial morphology of the dicynodont genus *Lystrosaurus*.—*Ann. S. Afr. Mus.* 56: 155–274.
- CLUVER, M. A. 1974. The skull and mandible of a new cistecephalid dicynodont.—*Ann. S. Afr. Mus.* 64: 137–155.
- COX, C. B. 1964. On the palate, dentition and classification of the fossil reptile *Endothiodon* and related genera.—*Am. Mus. Novit.* 2171: 1–25.
- CROMPTON, A. W. & HOTTON, N. 1967. Functional morphology of the masticatory apparatus of two dicynodonts (Reptilia, Therapsida).—*Postilla* 109: 1–51.
- EWER, R. F. 1961. The anatomy of the anomodont *Daptocephalus leoniceps* (Owen).—*Proc. zool. Soc. Lond.* 136: 375–402.
- GALTON, P. M. 1973. The cheeks of ornithischian dinosaurs.—*Lethaia* 6: 67–89.
- HAUGHTON, S. H. & BRINK, A. S. 1954. A bibliographic list of Reptilia from the Karroo beds of South Africa.—*Palaeont. afr.* 2: 1–187.
- KEYSER, A. W. 1973. A preliminary study of the type area of the *Cistecephalus* zone of the Beaufort Series, and a revision of the anomodont family Cistecephalidae.—*Mem. geol. Surv. Rep. S. Afr.* 62: 1–72.
- KITCHING, J. W. 1972. A short review of the Beaufort zoning in South Africa. In: INTERNATIONAL UNION OF GEOLOGICAL SCIENCES. *Commission on Stratigraphy. Subcommission on Gondwana Stratigraphy and Palaeontology. Gondwana Symposium 2nd, South Africa, 1970. Proceedings and papers*: 309–311. Pretoria: CSIR.
- ROMER, A. S. 1966. *Vertebrate paleontology*. Chicago: University of Chicago Press.
- TOERIEN, M. J. 1953. The evolution of the palate in South African anomodonts, and its classificatory significance.—*Palaeont. afr.* 1: 49–117.

ABBREVIATIONS

add. ext. lat.	. lateral division of external adductor muscle
add. ext. med.	. medial division of external adductor muscle
add. post.	. posterior adductor muscle
ang.	. angular
art.	. articular
boc.	. basioccipital

ch.	cheek
cor. proc.	coronoid process
den.	dentary
den. sh.	dentary shelf
ect.	ectopterygoid
eoc.	exoccipital
for. mag.	foramen magnum
ipt. vac.	interpterygoidal vacuity
jug.	jugal
lac.	lacrimal
lac. for.	lacrimal foramen
lat. den. sh.	lateral dentary shelf
lat. pal. for.	lateral palatal foramen
max.	maxilla
max. sh.	maxillary shelf
med. pm. r.	median premaxillary ridge
nas.	nasal
no.	notch
pa.	parietal
pal.	palatine
pin. for.	pineal foramen
pm.	premaxilla
po.	postorbital
post. pt.	posterior pterygoideus muscle
ps.	pseudotemporalis muscle
pt.	pterygoid
q.	quadrate
qj.	quadratejugal
q. ram.	quadrate ramus of pterygoid
sa.	surangular
sq.	squamosal
st.	stapes
vo.	vomer
AM	Albany Museum, Grahamstown
AMNH	American Museum of Natural History, New York
BMNH	British Museum (Natural History), London
SAM	South African Museum, Cape Town